

Toward Ecologically Scaled Landscape Indices

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ABSTRACT: Nature conservation is increasingly based on a landscape approach rather than a species approach. Landscape planning that includes nature conservation goals requires integrated ecological tools. However, species differ widely in their response to landscape change. We propose a framework of ecologically scaled landscape indices that takes into account this variation. Our approach is based on a combination of field studies of spatially structured populations (metapopulations) and model simulations in artificial landscapes. From these, we seek generalities in the relationship among species features, landscape indices, and metapopulation viability. The concept of ecological species profiles is used to group species according to characteristics that are important in metapopulations' response to landscape change: individual area requirements as the dominant characteristic of extinction risk in landscape patches and dispersal distance as the main determinant of the ability to colonize patches. The ecological profiles and landscape indices are then integrated into two ecologically scaled landscape indices (ESLI): average patch carrying capacity and average patch connectivity. The field data show that the fraction of occupied habitat patches is correlated with the two ESLI. To put the ESLI into a perspective of metapopulation persistence, we determine the viability for six ecological profiles at different degrees of habitat fragmentation using a metapopulation model and computer-generated landscapes. The model results show that the fraction of occupied patches is a good indicator for metapopulation viability. We discuss how ecological profiles, ESLI, and the viability threshold can be applied for landscape planning and design in nature conservation.

Keywords: landscape ecology, metapopulation, fragmentation, ecological profiles, landscape indices, viability threshold.

In landscapes where natural habitats have been severely fragmented by intensive farming and urbanization, bio-

diversity conservation is a growing issue in landscape planning and management. Networks of nature reserves are being proposed as a solution when the degree of fragmentation is considered to endanger the long-term persistence of target species (NPP 1990; European Union 1992; Opdam 2000). Landscape managers and conservation planners need tools that link landscape characteristics to some critical measure of the sustainable conservation of biodiversity values. The biggest problem is how to integrate habitat network requirements of an array of species that greatly differ in their response with landscape pattern and change because of different spatial requirements and different movement capacities (Lord and Norton 1990; Opdam 1990; Opdam et al. 1993; Noon et al. 1997).

Four approaches to this problem have been used. First, landscape indices, quantitative measures of landscape pattern, have been widely proposed (e.g., Franklin and Forman 1987; O'Neill et al. 1988a; Turner et al. 1989; Ripple et al. 1991; McGaral and Marks 1995; Gustafson 1998). The strength of landscape indices is their straightforwardness, but their weakness is the lack of any explicit relationship to ecological processes. Such indices do not take into account differences in the scale at which species respond to landscape structure. Second, strategic models (May 1973) have been used that produce simple rules of thumb such as extinction thresholds (e.g., Levins 1970; Lande 1987; Quinn and Hastings 1987; Fahrig 1990; Wissel and Stoecker 1991). Although these rules, based on general ecological mechanisms, provide a sound framework for addressing the problem, they are of no practical use because they lack an explicit link to real landscapes and often neglect species-specific responses to landscape scale. Third, empirical studies are conducted (see for reviews Harrison 1991, 1994; Opdam 1991; Reich and Grimm 1996; Harrison and Taylor 1997), in most of which species attributes are linked to landscape pattern using single-year distribution or turnover patterns. These produce regression models that usually are hard to extrapolate to other landscape areas and to the long-term chance of persistence (Ter Braak et al. 1998). Fourth, a modeling approach uses calibrated tactical models to link the landscape pattern to population viability (Lande 1987; Doak 1989; Verboom et al. 1991a; Hanski 1994b; Lindenmayer and Lacy 1995; Lin-

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denmayer and Possingham 1995; Sjögren-Gulve and Ray 1996; Thomas and Hanski 1997; Vos et al. 2000). Although ecologically sound, the weaknesses of this approach are the large amounts of required data and the focus on single species. Furthermore, these tactical models yield no general results (May 1973).

A new approach, combining the strengths and overcoming the weaknesses of existing methods, is needed. Essentially, this approach focuses on the variation among species by classifying species according to their response to habitat fragmentation. Although this has been attempted by using model simulations to group species according to their sensitivity to fragmentation (Andrén 1996) and by proposing “ecological profiles for colonization ability” (Grimm et al. 1996, p. 158), no empirical data were presented to underpin these model results. Grimm et al. (1996) ignored the fact that some species have strong responses to changes in patch area, while others are more susceptible to patch connectivity (*sensu* Fahrig and Merriam 1985).

In this article, we attempt to bridge the gap between empirical data (the first approach), single-species models (the fourth approach), and indices for habitat configuration at the landscape level (the first approach). In our approach, indicator species represent clusters of species (ecological profiles) differing in sensitivity to habitat fragmentation. We explore the performance of indicator species matrices with model simulations in computer-generated landscapes and predict metapopulation viability from occupation patterns of habitat networks. We propose ecologically scaled landscape indices (ESLI) as an alternative to general landscape indices. The usefulness of ESLI is tested with empirical data from the highly human-dominated landscapes in The Netherlands.

Introducing ESLI

Habitat fragmentation has two principal components: decrease in habitat area and increase in the isolation of the remaining habitat patches (Hanski and Gilpin 1991; Opdam et al. 1993). The incidence of a species in a patch (J) can be described as a function of colonization rate C and extinction rate E (Hanski 1994b):

$$J = C/(C + E). \quad (1)$$

The probability that a patch is occupied increases with growing colonization rate and decreases with increasing extinction rate. Since colonization rate is a function of patch isolation and extinction rate is a function of patch size, relatively small or isolated habitat patches are more likely to be empty (Opdam et al. 1993; Verboom et al. 1993; Reich and Grimm 1996; Noon et al. 1997). The

survival of a metapopulation (Levins 1970) depends on the colonization rate/extinction rate ratio of the patches. To determine a species' sensitivity to fragmentation, the key factors that determine the (area-dependent) extinction and (isolation-dependent) colonization probabilities must be known (Hanski 1994a). Two main factors primarily determine extinction risk: demographic and environmental stochasticity. For both types of stochasticity, extinction risk is closely linked to population size (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972; Den Boer 1981; Shaffer 1981; Gilpin and Soulé 1986; Goodman 1987; Mangel and Tier 1994; Foley 1997). For simplicity, we focus on characteristics that are related to population size and will not incorporate differences in sensitivity for environmental stochasticity. For a species in a fragmented landscape, average population size is determined by the individual area requirements in relation to patch size. In this article, we use individual area requirements (IAR, the area required for a reproductive unit, e.g., the territory of a pair of birds) as the key factor that differentiates between the sensitivity of species to patch size-related extinction risk. In relation to IAR, we define the carrying capacity K of a species s in a patch i , K_{si} as

$$K_{si} = \text{AREA}_i / \text{IAR}_{si}. \quad (2)$$

AREA_i is the area of patch i and IAR_{si} is the individual area requirements of species s in patch i . We propose the following index average patch carrying capacity as

$$\text{ESLI average patch carrying capacity} = \sum_{i=1}^n K_{si} / n, \quad (3)$$

the arithmetic mean of the K_{si} values in a landscape. The index combines the average patch size, a neutral (not ecologically scaled) landscape index, and the species-specific individual area requirement and is therefore an ecologically scaled landscape index (ESLI). In the same landscape, a species with small individual area requirements reaches a higher ESLI for average carrying capacity than a species with large individual area requirements.

To colonize habitat patches in a fragmented landscape, dispersing individuals must be able to reach habitat patches. Dispersal distance is highly variable among species (Hansson 1991; Stenseth and Lidicker 1992). For patch connectivity, we use the index C (Verboom et al. 1991a; Hanski 1994b):

$$C_{si} = \sum_{j=1}^n A_j \exp(-\alpha_s D_{ij}) \quad (j \neq i), \quad (4)$$

where C_{si} is the connectivity of a species s in a patch i ,

which is the sum of all contributions of patches j weighted both by their area (A_j) and the distance between patches i and j (D_{ij}). The contribution of a patch at distance D_{ij} declines exponentially with a species-specific parameter α_s (Verboom et al. 1991a; Hanski 1994b). The species-specific parameter α_s can be derived from knowledge about the dispersal distance distribution of the species: α can be set to a value that yields close to 0 contributions at distances beyond the maximum observed dispersal distance. We propose the index

$$\text{ESLI average patch connectivity} = \sum_{i=1}^n C_{si}/n, \quad (5)$$

the arithmetic mean value of C_{si} in a landscape. In contrast to other neutral (not ecologically scaled) connectivity indices, this index combines both species and landscape characteristics. In the same landscape, it will be higher for species with a large dispersal distance (small α_s) than for species with small dispersal distance (large α_s). Throughout this article, we will use log-transformed ESLI in graphs and statistical analyses.

Table 1 gives an example of six model species that span the ecological profiles for fragmentation sensitivity, combining different levels of individual area requirements and dispersal distances. The species with the largest individual area requirements and shortest dispersal distances is the

most sensitive to fragmentation (table 1, A). The most fragmentation-tolerant species is able to reach high densities and to disperse over large distances (table 1, F).

Performance of Model Species in Computer-Generated Landscapes

Methods

ESLI have significance for the conservation of biodiversity only if they can be linked to species viability for a variety of species and landscapes. We define a metapopulation in a landscape as viable if the habitat configuration combined with the species' characteristics yield an extinction probability of <5% over a 100-yr period (Shaffer 1981; Shaffer and Samson 1985). As a consequence of our definition of metapopulation viability, which includes both a large time span and a probabilistic character, we have chosen a stochastic simulation model that captures the complexity of both the landscape and the species dynamics. The modeling has a strategic goal (sensu Metz and De Roos 1992) using hypothetical species in artificial landscapes. The main objective is to explore the performance of ecological profiles under increasingly fragmented conditions.

The simulations were carried out with the metapopulation model METAPHOR (Verboom 1996; Verboom et al. 1999), developed in 1995 and used since then in several

Table 1: Six examples of ecological profiles for fragmentation sensitivity (A–F)

	Short dispersal distance .1–1 km $(\alpha_s = 5, \text{eq. [4]})^a$	Middle dispersal distance 1–3 km $(\alpha_s = 1.67, \text{eq. [4]})^a$	Large dispersal distance 3–10 km $(\alpha_s = .5, \text{eq. [4]})^a$
Indicator species for fragmentation sensitivity			
Large individual area requirements 1 r.u./ha ($\text{IAR}_s = 1, \text{eq. [2]})$	A Highest fragmentation sensitivity High extinction risk Low colonization ability	B High extinction risk Medium colonization ability	C High extinction risk Good colonization ability
Small individual area requirements 50 r.u./ha ($\text{IAR}_s = .02, \text{eq. [2]})$	D Low extinction risk Low colonization ability	E Low extinction risk Medium colonization ability	F Lowest fragmentation sensitivity Low extinction risk Good colonization ability

Note: Each ecological profile is a different combination of individual area requirements (IAR) and dispersal distance. IAR_s is a species (group) specific parameter for patch size-related extinction risk (see eq. [2]). α_s is a species (group) specific parameter for patch connectivity-related colonization ability (see eq. [4]). The six ecological profiles correspond with the six model species used in the simulations. r.u. = reproductive unit.

^a Maximum dispersal distance covered by the main body of dispersers.

Table 2: A summary of the empirical data

Species	Habitat (%)	Occupied fraction	Regression analysis		Reference
			Patch size	Connectivity	
Nuthatch (<i>Sitta europea</i>)	1.5	.42	***	***	Verboom et al. 1991a
Reed warbler (<i>Acrocephalus scirpaceus</i>)	.2	.67	***	***	Foppen and Chardon 2000
Root vole (<i>Microtus oeconomus</i>):					
Goeree (1)	2.18	.71	NS	NS	Bergers et al. 1994
Schouwen (2)	.36	.59	NS	*	Bergers et al. 1994
Trunk ant (<i>Formica truncorum</i>)	.9	.24	**	*	Mabelis 1987
Bog bush cricket (<i>Metrioptera brachyptera</i>)	2.5	.51	***	*	Mabelis and Mekenkamp 1996
Meadow grasshopper (<i>Chorthippus parallelus</i>)	7.4	.72	***	NS	Mabelis and Mekenkamp 1996
Grayling (<i>Hipparchia semele</i>)	18	.57	***	NS	K. Verspui, unpublished manuscript
Green hairstreak (<i>Callophrys rubi</i>)	25	.89	*	NS	K. Verspui, unpublished manuscript
Silver-studded blue (<i>Plebejus argus</i>)	18	.34	***	NS	K. Verspui, unpublished manuscript
Tree frog (<i>Hyla arborea</i>)	1.4	.10	NS	***	Vos and Stumpel 1996
Moor frog (<i>Rana arvalis</i>)	11.2	.67	***	NS	Vos and Chardon 1998
Honeysuckle (<i>Lonicera periclymenum</i>)	16	.09	***	***	Grashof-Bokdam 1997
Bird cherry (<i>Prunus serotina</i>)	16	.09	***	NS	Grashof-Bokdam 1997

Note: For each species, the percentage of coverage of suitable habitat and the fraction of occupied patches in the study areas are listed with the results of logistic regression analysis on patch area and connectivity. References for more species-specific details are given. For the root vole, the results are from two different study cases and are given separately. NS = not significant.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

theoretical and applied studies (Reijnen et al. 1995; Bugter and Vos 1997). METAPHOR describes the spatial dynamics of a metapopulation in discrete time. The metapopulation is monitored once a year, and changes in the metapopulation are calculated yearly. Individuals have a chance to reproduce and to die (dynamics within a patch) or to disperse (dynamics between patches; see the appendix for a detailed model description). The model species modules were derived from calibrated modules for two bird species: European bittern (*Botaurus stellaris*) and reed warbler (*Acrocephalus scirpaceus*; Foppen et al. 1999). They were tuned to represent the six ecological profiles of table 1 by incorporating their dispersal characteristics and area requirements. All model species are territorial and monogamous. The model species with large individual area requirements has been given a relatively low density-dependent growth rate and low mortality. The species with small individual area requirement has been given a higher density-dependent growth rate, higher number of dispersers, and higher mortality. Some environmental stochasticity for species with small individual area requirements is incorporated as a higher standard deviation for birth and death rates. We calibrated roughly varying parameter values for dispersal probability, mortality during dispersal, and the standard deviation for birth and death rates until no model species always went extinct or always survived in the simulation landscapes. An overview of all parameter values is given in the (table A1).

The simulations were carried out in computer-generated landscapes of 100 km², with suitable habitat percentages of 0.5%, 1%, 2%, 4%, and 8% distributed over habitat patches of 1, 2, 4, 8, and 16 ha (table A2). The number of patches per simulation landscape varied from seven to 50 (table A2). The low percentage of suitable habitat in the simulation landscapes reflects the habitat coverages in the empirical studies (table 2). The low fraction of suitable habitat is also determined by the focus on viability thresholds in this study. The patches were distributed randomly by a landscape generator, keeping a minimal distance between patch edges of 1.5 times the home range size of the species with the largest area requirements. For each combination of habitat percentage and patch size, one landscape was generated. To keep the number of landscape-species combinations at a manageable level, patch size was kept constant in a simulation landscape. One hundred runs per simulation were conducted for each landscape-species combination. A run started with all patches occupied up to carrying-capacity level and ran for 150 time steps. Based on visual estimates from several time series, the pattern of occupancy no longer depended on the initial distribution after 50 time steps. Therefore, time steps 51–150 were used in the analyses, as the pattern of occupancy was presumed to be the result of a quasi equilibrium between species and landscape characteristics. Metapopulation viability was determined by calculating the extinction probability of the metapopulation during

the 100 runs. The average fraction of occupied patches during the period the metapopulation was extant was calculated as an ecological measure of fragmentation effects (Levins 1970). The percentage of suitable habitat is given as a neutral landscape index of fragmentation, linking our approach to previous literature (O'Neill et al. 1988b; Gustafson and Parker 1992; Gustafson 1998). To explore the viability of the metapopulations in the combinations of model species and simulation landscapes, the extinction probability was analyzed with logistic regression analysis (Jongman et al. 1995) using the average fraction of occupied patches and the life-history parameters of the model species as explanatory variables.

Model Species Dynamics

Simulation results are presented in figures 1 and 2. As expected, the mean fraction of occupied patches increased for each model species with increasing percentage of suitable habitat and increasing patch size (fig. 1). Differences between the model species were as anticipated. Larger dispersal distances increased the fraction of occupation for both species with large individual area requirements (cf. fig. 1A, 1B, and 1C) and for species with small individual area requirements (cf. fig. 1D, 1E, and 1F). The species with small individual area requirements had a higher degree of occupation in similar landscapes, with similar dispersal distances compared to species with large individual area requirements (cf. fig. 1A with 1D, 1B with 1E, and 1C with 1F).

The extinction probability of the metapopulation decreased with increasing habitat percentage and increasing

patch size (fig. 2). Small individual area requirements and increasing dispersal distance had a positive effect on the survival probability. The model species with the highest fragmentation sensitivity, large individual area requirements, and small dispersal distance became extinct in most simulation landscapes. The most fragmentation-tolerant model species, with small individual area requirements and large dispersal distance, had the highest survival probability in most landscapes (cf. fig. 2A and 2F). Hence, our assumption holds that the ecological profiles characteristics (table 1) are related to fragmentation sensitivity and that the fragmentation-tolerant species can survive in a wider range of landscape structures than fragmentation-sensitive species.

Metapopulation Viability Threshold

In the logistic regression analysis of the extinction probability, both the fraction of occupied patches and the factor model species were significant ($P < .001$). The fraction occupied patches explained 340 times more variance per degree of freedom than the factor model species and was therefore kept as the only predictor for the extinction probability. The extinction probability decreased with increasing fraction of occupied patches (fig. 3) and is $<5\%$ in 100 yr when the fraction of occupied patches is ~ 0.5 or higher. Thus, the metapopulation is viable when the fraction of occupied patches is ~ 0.5 or higher, which can be regarded as a viability threshold (fig. 3). The 95% confidence interval for this threshold is 0.45–0.6. We conclude that the model predicts that a metapopulation is viable if the fraction of occupied patches is >0.6 and nonviable

A. Large individual area requirement Short dispersal distance						
habitat [%]	patch size	patch size				
		1	2	4	8	16
0.5		0.00	0.00	0.00	0.07	
1			0.00	0.01	0.15	0.55
2				0.01	0.18	0.63
4					0.24	0.68
8						0.77

B. Large individual area requirement Middle dispersal distance						
habitat [%]	patch size	patch size				
		1	2	4	8	16
0.5		0.00	0.01	0.04	0.34	
1			0.00	0.07	0.39	0.71
2				0.05	0.53	0.77
4					0.64	0.89
8						0.96

C. Large individual area requirement Large dispersal distance						
habitat [%]	patch size	patch size				
		1	2	4	8	16
0.5		0.00	0.01	0.13	0.79	
1			0.00	0.11	0.77	0.99
2				0.10	0.90	0.95
4					0.93	0.99
8						1.00

D. Small individual area requirement Short dispersal distance						
habitat [%]	patch size	patch size				
		1	2	4	8	16
0.5		0.01	0.03	0.07	0.67	
1			0.11	0.37	0.70	1.00
2				0.29	0.78	1.00
4					0.87	1.00
8						1.00

E. Small individual area requirement Middle dispersal distance						
habitat [%]	patch size	patch size				
		1	2	4	8	16
0.5		0.16	0.56	0.99	0.85	
1			0.74	1.00	0.95	1.00
2				0.97	1.00	1.00
4					1.00	1.00
8						1.00

F. Small individual area requirement Large dispersal distance						
habitat [%]	patch size	patch size				
		1	2	4	8	16
0.5		0.39	0.96	1.00	1.00	
1			0.98	0.99	1.00	1.00
2				1.00	1.00	1.00
4					1.00	1.00
8						1.00

Figure 1: Average fraction of occupied patches during the period the metapopulation was extant in relation to patch size and habitat percentage of the simulation landscapes for the six model species (A–F).

A. Large individual area requirement Short dispersal distance						
habitat [%]	patch size					
	1	2	4	8	16	
0.5	1.00	1.00	1.00	0.98		
1		1.00	0.97	0.54	0.01	
2			1.00	0.31	0.00	
4				0.03	0.00	
8					0.00	

B. Large individual area requirement Middle dispersal distance						
habitat [%]	patch size					
	1	2	4	8	16	
0.5	1.00	1.00	0.98	0.56		
1		1.00	0.92	0.02	0.00	
2			0.93	0.00	0.00	
4				0.00	0.00	
8					0.00	

C. Large individual area requirement Large dispersal distance						
habitat [%]	patch size					
	1	2	4	8	16	
0.5	1.00	1.00	0.97	0.00		
1		1.00	0.96	0.01	0.00	
2			1.00	0.00	0.00	
4				0.00	0.00	
8					0.00	

D. Small individual area requirements Short dispersal distance						
habitat [%]	patch size					
	1	2	4	8	16	
0.5	0.97	0.94	0.99	0.17		
1		0.27	0.00	0.00	0.00	
2			0.10	0.00	0.00	
4				0.00	0.00	
8					0.00	

E. Small individual area requirements Middle dispersal distance						
habitat [%]	patch size					
	1	2	4	8	16	
0.5	0.42	0.01	0.00	0.00		
1		0.02	0.00	0.00	0.00	
2			0.00	0.00	0.00	
4				0.00	0.00	
8					0.00	

F. Small individual area requirements Large dispersal distance						
habitat [%]	patch size					
	1	2	4	8	16	
0.5	0.83	0.05	0.00	0.00		
1		0.01	0.00	0.00	0.00	
2			0.00	0.00	0.00	
4				0.00	0.00	
8					0.00	

Figure 2: Extinction probability of the metapopulation in relation to patch size and habitat percentage of the simulation landscapes for the six model species (A–F).

when it is <0.45 . This prediction rule gave five mismatches (6%) in the simulation data. In three simulations, the metapopulation was wrongfully judged nonviable and in two simulations, viable.

Testing ESLI to Empirical Data

The empirical studies were carried out in the extremely fragmented landscapes of The Netherlands—fragmentation mainly due to human activities—with percentages of suitable habitat ranging from 0.2 to 25 (table 2). Empirical data come from a wide range of species: birds, mammals, insects, amphibians, and plants. Data collection methods—except for species-specific inventory methods—were similar, so results are valid for between-species comparison. Details of the studies are available as follows: birds (nuthatch [*Sitta europea*], Verboom et al. 1991a; and reed warbler [*Acrocephalus scirpaceus*], Foppen and Chardon 2000); mammals (root vole [*Microtus oeconomus*], Bergers et al. 1994); insects (ants: trunk ant [*Formica truncorum*], Mabelis 1987; grasshoppers: meadow grasshopper [*Chorthippus parallelus*] and bog bush cricket [*Metrioptera brachyptera*], Mabelis and Mekenkamp 1996; and butterflies: green hairstreak [*Callophrys rubi*], silver-studded blue [*Plebejus argus*], and grayling [*Hipparchia semele*], K. Verslui, unpublished manuscript); amphibians (tree frog [*Hyla arborea*], Vos and Stumpel 1996; and moor frog [*Rana arvalis*], Vos and Chardon 1998); and plants (honeysuckle [*Lonicera periclymenum*] and bird cherry [*Prunus serotina*], Grashof-Bokdam 1997). Each study made an inventory of all potential suitable habitat patches, and collected presence data are summarized in table 2. All suitable

patches were searched several times under favorable inventory conditions to minimize the chance that occupied patches were classified as unoccupied (see species-specific references). Both occupied and unoccupied patches were found in all studies.

To test effects of habitat fragmentation, the distribution pattern was analyzed by logistic regression. In the regression analysis, habitat-quality factors were first entered in the model. Subsequently, to test whether fragmentation variables were additional explanatory factors (Van Apeldoorn et al. 1992; Fahrig et al. 1995; Vos and Stumpel 1996), the model was extended with an area variable patch size and a connectivity variable depending on the dispersal distance of the species (see eq. [2]). Except for the root vole on the island of Goeree (Bergers et al. 1994), logistic regression analysis of the distribution pattern revealed significant effects of habitat fragmentation in all studies. However, in only five of the 14 studies was the probability of occupancy related to both patch size and connectivity (table 2).

Although the fraction of occupation differs widely between species (table 2), there seemed to be no relation with the neutral landscape indices mean patch size and percentage of suitable habitat (fig. 4). For example, there was a very low degree of occupancy (0.09) in honeysuckle and bird cherry, although the percentage of suitable habitat (16%) is relatively high. In contrast, the reed warbler was found in a much higher fraction (0.67) in a landscape with only 0.5% suitable habitat (fig. 4). So the neutral landscape index—fraction of suitable habitat remaining—cannot be applied as a predictor of metapopulation viability for all species.

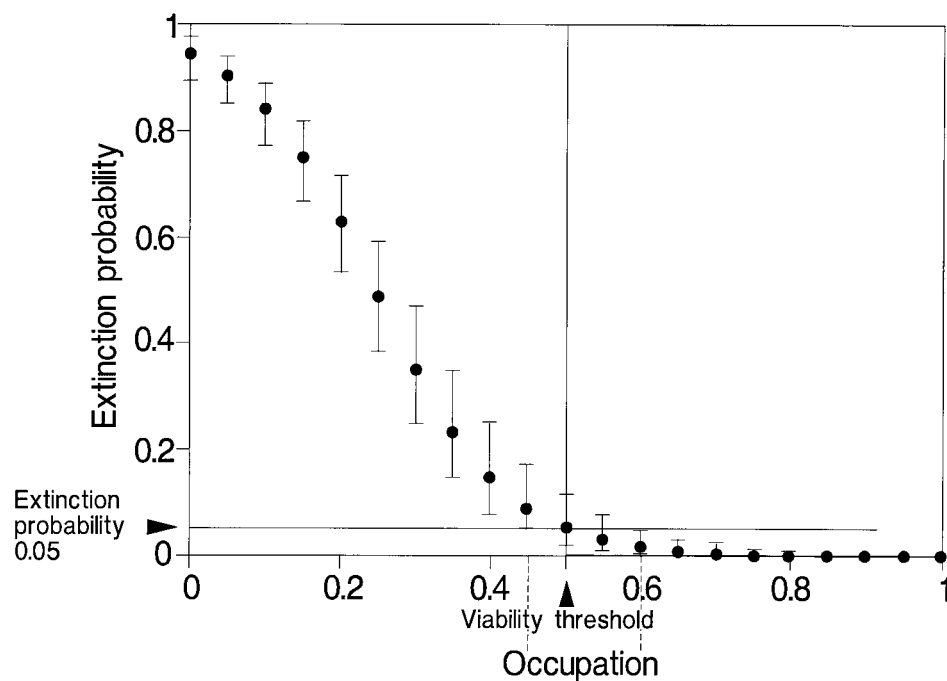


Figure 3: Viability of the metapopulations in the model simulations was analyzed with logistic regression analysis. Predicted relationship between the average fraction of occupied patches and the extinction probability of the metapopulation is shown. Extinction probability is <5% in 100 yr when the fraction of occupation is >0.5. Viability threshold at 0.5 fraction of occupied patches is indicated. The 95% confidence interval is 0.45–0.6.

What picture emerges if the neutral landscape indices are rescaled into ESLI, in which species differences for fragmentation sensitivity are incorporated? In table 3, the species are grouped according to their estimated individual habitat area requirements and their maximum dispersal distance, the distance that will be covered by the main body of dispersers. These estimations are based on field observations, literature, and expert knowledge. The 13 species can be grouped into nine different ecological profiles based on their individual area requirements and dispersal distance (table 3). Six species have ecological profiles that coincide with those of the model indicator species (table 3, models A, C, D, and F). The profiles of the other seven species have either a smaller individual area requirement (with a maximum of 1,000–10,000 reproductive units/ha of the meadow grasshopper) or a smaller dispersal distance (e.g., honeysuckle: <0.1 km, $\alpha = 50$; table 3).

ESLI of average patch carrying capacity and average patch connectivity were calculated for each species landscape combination (eqq. [3] and [5]; table 3). The standard deviation of the values that are averaged to obtain the ESLI are very high, notably for the silver-studded blue and the meadow grasshopper (table 3). A possible explanation for this is the presence of a large mainland patch or source patch in the landscape (Harrison 1991), a feature that was

not incorporated in our simulation models, where patch size per simulation landscape was held constant. When arranging the species in a graph with the ESLI on the axes, the fraction of occupied patches positively correlates (fig. 5). The silver-studded blue deviates from this general trend by having a small occupied fraction (0.34) in contrast to the high connectivity and carrying capacity of its landscape. In a logistic regression of the fraction of occupied patches on the ESLI, without this outlier, both indices are significant ($P < .05$). Species in the left bottom side of the graph (fig. 5) are those that will suffer most from habitat fragmentation: their low connectivity results in low colonization chances, and their small populations have a high extinction risk. These species have very low values for patch occupancy. The fraction of occupied patches gradually increases with increasing connectivity and carrying capacity per patch, with the highest occupancy in the top right corner of the graph.

Since the ESLI account for species-specific dispersal distance and individual area requirements, species can have quite different values with similar amounts of habitat; compare, for example, the figures of the nuthatch and the tree frog (table 2; fig. 5). The reason for relatively high patch occupation in the reed warbler (0.67) in a landscape with only 0.2% of suitable habitat now becomes clearer.

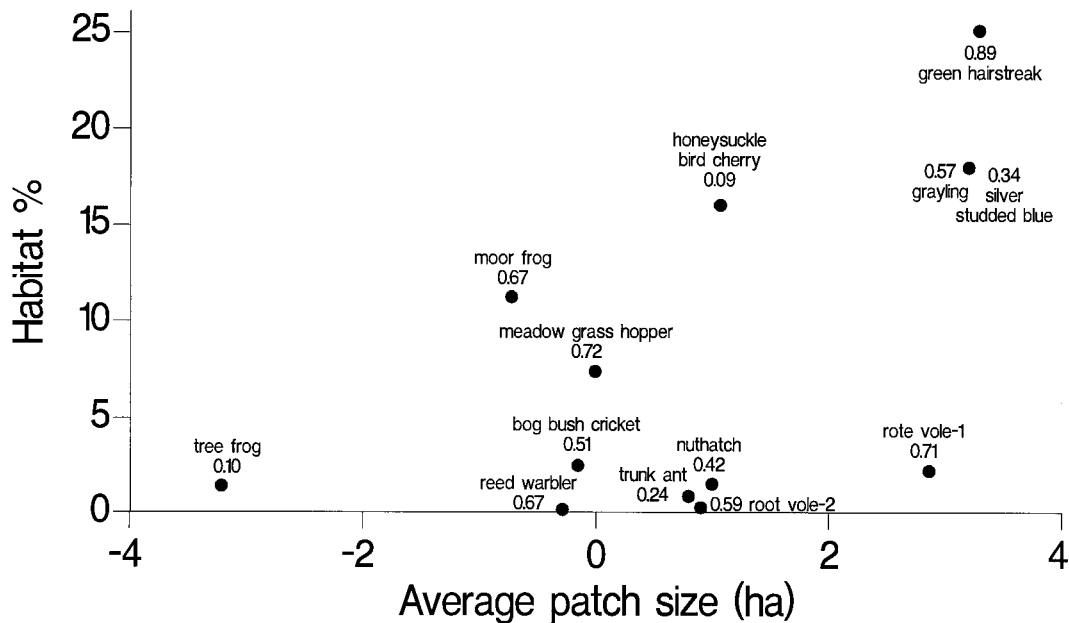


Figure 4: Arrangement of the empirical data according to two neutral landscape indices: the percentage of suitable habitat and the (log-transformed) average patch size of the study areas. Each point in the graph represents a species-landscape combination. For each species, the observed fraction of occupied patches is indicated.

The reed warbler has the most fragmentation-tolerant profile and so has relatively high ESLI values even in an extremely fragmented landscape. In general, the relationship of increasing values of the ESLI and increasing patch occupation holds for a broad range of species in the empirical studies. The empirical data do suggest that differences in fragmentation sensitivity between species should be sufficiently incorporated in the ESLI. The ESLI can therefore be applied for comparisons between species.

The prediction rule for metapopulation viability, derived from the simulation data, implies that the metapopulations of five of the species (trunk ant, silver-studded blue, tree frog, honeysuckle, and bird cherry) used in the empirical analyses are nonviable, whereas one species (nuthatch) is on the edge of nonviability.

Discussion

Why Use Ecologically Scaled Landscape Indices?

Both the empirical data and the model results illustrate that species have different scale-dependent responses to landscape fragmentation. It follows that any landscape index that fails to account for this scale-dependent variation has no ecological significance. These include the neutral measures proposed by, among others, Franklin and Forman (1987), O'Neill et al. (1988a), Turner et al. (1989), Ripple et al. (1991), McGarrigal and Marks (1995), and

Gustafson (1998). Similarly, there is no universally applicable viability threshold at a fixed percentage of suitable habitat. Therefore, it follows that applying the commonly used landscape index fraction of suitable habitat (O'Neill et al. 1988b; Gustafson and Parker 1992; Andrén 1994, 1996; Venier and Fahrig 1996; Gustafson 1998) as a universal predictor of metapopulation persistence is not ecologically valid.

Landscape indices can be indicators for the fraction of occupied habitat and indirectly for metapopulation viability but only if these indices are ecologically scaled. Our empirical data show a positive correlation between the fraction of occupied habitat patches (an important predictor of metapopulation viability) and the ecologically scaled landscape indices (ESLI) proposed in this article. Therefore, we conclude that ecological profiles and ESLI are useful tools for integrated fragmentation assessment and for making predictions about the spatial conditions of the landscape for sustainable conservation of biodiversity.

By distinguishing ecological profiles for extinction risk and colonization ability, we have shown that the ecological variation encompassed by species in landscapes can be effectively reduced. We have shown that, using the model species, these ecological profiles can be linked to viability thresholds at different levels of fragmentation. The resulting matrix of ecological profiles, classified according

Table 3: Ecological profiles and ecologically scaled landscape indices (ESLI) for species in the empirical data set

Fragmentation sensitivity and species	Ecological profile				ESLI			
	IAR _s (r.u./ha)	Maximum dispersal distance (km) ^a	α_s	Model species	Average patch carrying capacity \pm SD		Average patch connectivity \pm SD	
1: Honeysuckle (<i>Lonicera periclymenum</i>)	1–10	<.1	50	...	17.40 \pm	197.00	.07 \pm	4.40
2: Trunk ant (<i>Formica trunctorum</i>)	1 nest	.1–1	5	A	2.20 \pm	5.85	.80 \pm	.67
3: Bird cherry (<i>Prunus serotina</i>)	1–10	.1–1	5	...	17.40 \pm	197.00	.28 \pm	8.52
4: Root vole (<i>Microtus oeconomus</i>):								
Goeree (1)	10–100	1–3	1.67	D	983.14 \pm	3,973.50	36.11 \pm	72.07
Schouwen (2)	10–100	1–3	1.67	D	136.86 \pm	506.21	2.55 \pm	6.62
Grayling (<i>Hipparchia semele</i>)	10–100	1–3	1.67	D	1,372.00 \pm	8,330.36	138.10 \pm	267.56
Green hairstreak (<i>Callophrys rubi</i>)	10–100	1–3	1.67	D	1,504.72 \pm	10,022.75	117.59 \pm	284.91
5: Silver-studded blue (<i>Plebejus argus</i>)	100–1,000	.1–1	5	...	13,499.50 \pm	81,964.79	84.44 \pm	245.26
Bog bush cricket (<i>Metrioptera brachyptera</i>)	100–1,000	.1–1	5	...	469.34 \pm	2,259.03	.25 \pm	.91
6: Tree frog (<i>Hyla arborea</i>)	100–1,000	1–3	1.67	...	22.68 \pm	65.52	.28 \pm	.18
Moor frog (<i>Rana arvalis</i>)	100–1,000	1–3	1.67	...	268.80 \pm	90.31	1.05 \pm	.99
7: Meadow grasshopper (<i>Chorthippus parallelus</i>)	1,000–10,000	.1–1	5	...	5,413.53 \pm	26,018.43	6.98 \pm	7.45
8: Nuthatch (<i>Sitta europea</i>)	1	3–10	.5	C	2.70 \pm	6.44	64.00 \pm	25.50
9: Reed warbler (<i>Acrocephalus scirpaceus</i>)	10–100	3–10	.5	F	42.00 \pm	200.89	3.43 \pm	4.85

Note: Classes of individual area requirements (IAR_s), the species (group) specific parameter for patch size–related extinction risk, are listed (see also eq. [2] in text). The species (group) specific dispersal distance and the dispersal distance–related α_s , the parameter for patch connectivity related colonization ability, are listed (eq. [4]). Species are listed in order of fragmentation sensitivity, starting with the most fragmentation-sensitive profile. Nine different ecological profiles are distinguished. Model species with similar ecological profiles are indicated as A, C, D, or F. The ESLI average patch carrying capacity (eq. [3]) and average patch connectivity (eq. [5]) are given. r.u. = reproductive unit.

^a Covered by the main body of dispersers.

to individual area requirements and dispersal distance, encompasses relevant elements of this specific scale-dependent fragmentation sensitivity. Accordingly, Andrén (1996) demonstrated that fragmentation and viability

thresholds vary across species and landscapes by using an incidence function metapopulation model (Hanski 1994b; Ter Braak et al. 1998) that is spatially explicit but neglects local dynamics.

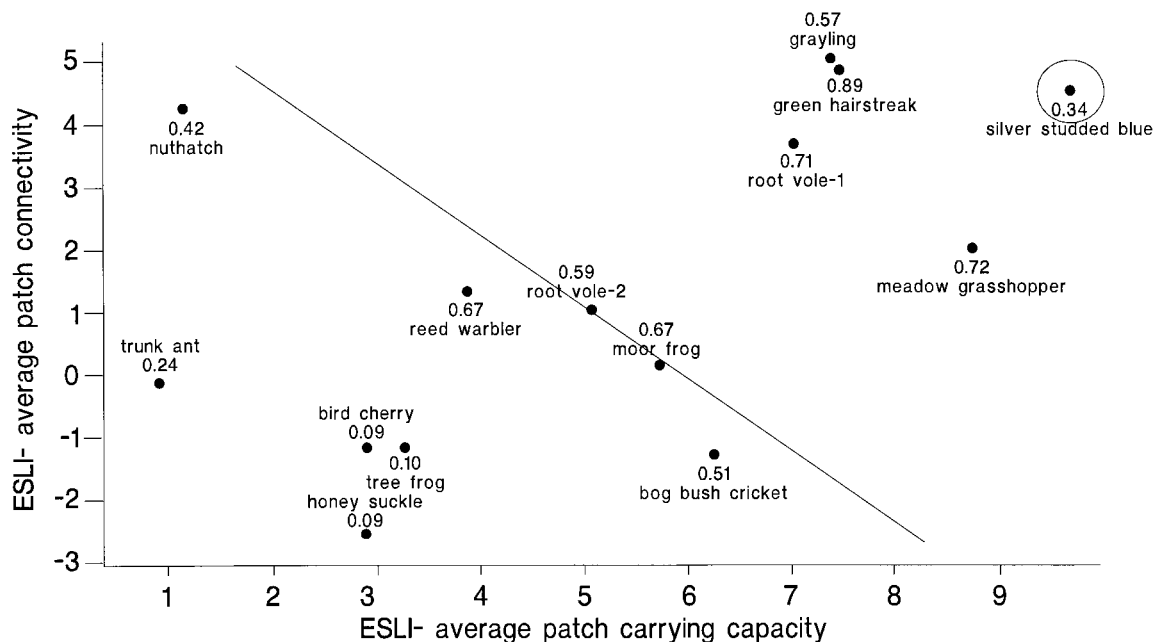


Figure 5: Arrangement of the empirical data according to the (log-transformed) ecologically scaled landscape indices (ESLI) for average patch carrying capacity and average patch connectivity using equations (3) and (5) (see text and table 3). Each point on the graph represents a species-landscape combination, and the observed fraction of occupied patches is indicated. The isoline of 0.5 fraction of occupation, the viability threshold, is estimated with logistic regression analysis with the two ESLI as explanatory variables.

Fraction of Occupied Patches as a Universal Predictor for the Effect of Fragmentation?

Our model results corroborate the suggestion by Hanski (1994a, 1994b) that the fraction of occupied patches is a useful predictor of metapopulation viability. In nonviable metapopulations (*sensu* Shaffer 1981), the fraction of occupied patches drops below 0.5 with confidence limits of 0.45–0.60 (fig. 3). The fraction of occupied patches in a landscape results from interactions between landscape characteristics and species characteristics. One would therefore expect that species characteristics also influence metapopulation viability. However, species characteristics explained little extra variation in the logistic regression of the simulation results. We therefore propose the fraction of occupied patches as a universal yardstick for fragmentation effects. The 50% metapopulation occupation threshold might be a universal empirical indicator for a serious conservation threat due to habitat fragmentation. It is important to stress that the landscapes in which species reach this occupation fraction differ widely and that the effect is the combined result of the interplay of species and landscape characteristics (as expressed in the ESLI).

A universal viability threshold linked to the fraction of occupied suitable patches would be a very strong (and useful) tool for conservation planning. Its robustness

should therefore be further tested for other combinations of landscape configurations and other ecological profiles. Nevertheless, it seems likely that metapopulations that occupy fractions of suitable patches far below the viability threshold of 0.5 are seriously threatened. A direct extrapolation from the relationship between the fraction of occupied patches and the extinction probability in the model simulations suggests that for five of the 14 species we discuss here (table 2), the metapopulations are nonviable.

There are, however, some qualifications to this general rule. First, the simulation landscapes in this study had patches of equal size. Thus the fraction of occupied patches is strongly correlated with the fraction of occupied habitat. In real landscapes, of course, patches vary in size. Large patches tend to be occupied more often than small patches. If a habitat network consists of a very large occupied patch and several small and unoccupied ones, the fraction of occupied patches is low, while the single large population may be viable on its own. In general, variation in patch size will increase metapopulation viability, and the rule of thumb based on the fraction of occupied patches will become more complex if patches of unequal size are incorporated.

Second, the total number of patches in the simulation landscape (seven to 50 patches) was small. Because the

probability of chance extinctions increases as the number of occupied patches decreases (Verboom et al. 1991*b*), simulations should be extended to variable metapopulation size.

Third, the interpretation of occupancy data in empirical studies can lead to overoptimistic viability predictions because of the time lag between habitat loss and species loss (Nee 1994; Tilman et al. 1994; Harrison and Taylor 1997). Figure 3 is based on the average occupancy over 100 yr of simulation, starting from year 51, with the assumption that over this period the metapopulation was in dynamic quasi equilibrium with the landscape. However, in the past 100 yr, the landscapes of the empirical studies have witnessed a progressive fragmentation (Vos and Zonneveld 1993). Therefore, the observed patterns of occupancy may relate to the landscape of the past more than to the landscape of the present. This ghost of the landscape past problem is especially likely to occur in situations where turnover rates are low, such as invertebrates in large patches (De Vries 1996) and plants with large generation times, such as honeysuckle and bird cherry (Grashof-Bokdam 1997).

Given the low fraction of occupancy found in our empirical studies, it is remarkable that in only five cases the distribution pattern could be explained by both an area and a connectivity effect in regression analysis. The six studies in which an area effect but no connectivity effect was found need careful evaluation because we cannot rule out a passive sampling effect as an alternative explanation of the distribution pattern (Verboom et al. 1991*a*; Andr  n 1994). A passive sampling effect is the increasing probability of occupation with increasing patch area due to the fact that the probability of finding one or more individuals in a patch of a certain size is a function of the patch size, even if individuals were randomly distributed in space (Verboom et al. 1991*a*; Andr  n 1994). It is also possible that a species suffers from fragmentation, but for statistical or ecological reasons, this is not detectable (e.g., too small field samples, too little variation in the explanatory variables, correlation between habitat quality and fragmentation variables, species interaction).

Improving Ecological Profiles and ESLI

We consider that developing ecological profiles and ESLI is a valuable step toward establishing general rules for the relationship between biodiversity and landscape pattern. Our framework now needs to be more thoroughly tested, both with more empirical data and more extensive exploration of model species and landscape configurations.

The ESLI of average patch carrying capacity and average patch connectivity were calculated for the model species landscape combinations. As expected, when comparing re-

sults within species, the fraction of occupation positively correlates with ESLI values. However, when we compared the results between species, or compared empirical data with model results, a discrepancy emerged. Model results such as mean occupancy are extremely sensitive to the exact value of input parameters like mortality and amount of variation (Goodman 1987; Verboom et al. 1993). In real species, life-history parameters are related (e.g., Comins et al. 1980). In our selection of parameter values for the model species, we did not take these relations into account quantitatively, and, consequently, unrealistic parameter combinations could have been chosen. Our calibration method enhanced this effect as we did not accept parameters that yielded 100% survival or 100% extinction in all landscapes. Therefore, the exact quantitative outcome of the models is trivial, and only a comparison within species is allowed. This mismatch has no consequence for the relation between model results such as patch occupancy and extinction probability. The latter was shown to depend little on specific parameter values. This certainly asks for further simulations, and applying models calibrated on empirical data for different species would circumvent this problem.

Mean patch carrying capacity and mean patch connectivity formed the basis of our ESLI to describe the habitat configuration in the landscape. These statistics are a selection out of many possible patch indices (e.g., Gustafson 1998) and do not take variance in patch size and patch connectivity into account. In particular, the presence of large source or mainland patches will improve population viability (Hanski et al. 1996). We explored ESLI that do correct the mean for variance, $E + V/E$ (Adler and N  r  nberger 1994), in which E stands for mean connectivity or carrying capacity and V stands for variance in connectivity or carrying capacity. However, this did not improve the correlation between fraction of occupation and ESLI values. Therefore, we selected the simplest and best performing ESLI, although further testing on more empirical data might indicate other indices are more useful than the mean value.

We did not incorporate sensitivity for environmental stochasticity in the ESLI. Although for some species, such as insects and, to some extent, amphibians and reptiles that are very sensitive to environmental stochasticity, even large populations have a real extinction risk (Gilpin and Soul   1986; Goodman 1987). Taking into account environmental stochasticity in a two-axis state, space is possible by further scaling of average patch carrying capacity. One could weigh ecological profiles by, for instance, equaling 1,000 butterflies and 10 large birds in terms of extinction rate. However, this would introduce an extra unknown weighting factor; therefore, we chose this model for simplicity.

Another aspect that could require incorporation is the mode of locomotion used during dispersal and the interaction with landscape pattern. In ground-dwelling species, the landscape mosaic influences the connectivity (Forman and Godron 1986; Opdam 1990; Merriam 1991; Saunders and Hobbs 1991; Wiens 1997; Bennett 1999; Vos et al. 2001). For these species, a correction for matrix resistance should be incorporated in the ESLI average connectivity.

Implications for Nature Conservation

The empirical data and model results indicate that for species and landscape characteristics, general rules can be developed in an ecologically sensible way. The definition of viability thresholds of indicator groups for fragmentation sensitivity would be a valuable tool for maintaining optimal species diversity in natural areas. Although the proposed tools for landscape managers and conservation planners are still in their infancy, we can now outline how the indicator groups and ESLI can, in principle, be applied. Even without exact information on the species' distribution, a landscape manager can detect fragmentation problems as follows: first, create a Geographic Information System map of habitat types and the interpretation of habitat suitability for characteristic species or target species; second, link the target species to indicator groups for fragmentation sensitivity based on knowledge about individual area requirements and dispersal distances (see, e.g., table 3); third, calculate the ESLI of the landscape for each indicator group–suitable habitat combination; fourth, find the position of the managed landscape for each indicator group (and corresponding target species) in the matrix of ESLI (see, e.g., fig. 5), and determine whether the species in the landscape is above or below its viability threshold.

This system also shows potential for landscape design through determining the domain that is above the viability threshold for relevant species profiles, for instance, expressed as average patch size and percentage of habitat coverage (e.g., table 2). Where complete census data are available, the percentage of occupation of suitable habitat patches can be used as an indicator of potential conservation problems of target species due to habitat fragmentation.

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APPENDIX A

The Simulation Model METAPHOR

METAPHOR is a spatially explicit, individual-based model that simulates the dynamics of a metapopulation. A simulation starts with a number of individuals of different age classes and sex categories in a number of patches. The default initiation is with each patch filled to carrying capacity. Mortality, reproduction, and dispersal determine the magnitude and structure of subpopulations and, thus, direct metapopulation dynamics. Carrying capacity is a linear function of patch area, truncated to discrete numbers.

At the start of a year, a census is taken. One could say that this is a prebreeding census, implying that individuals in the first age class are already almost 1 yr old. The first event in the new year is reproduction. Next, mortality occurs. Then, individuals move to the next age class. Finally, dispersal takes place. Mortality and recruitment are density dependent as shown in figure A1.

Mortality risk is calculated on an annual basis. Mortality probability in patch i is made up of a background mortality component, affected by environmental variability, and a density-dependent component, depending on local population density (per sex). In this application, all patches have equal quality, and the environment is equal for all patches in any year: the environmental variation is perfectly correlated for all patches, age classes, and both sexes.

Mortality, for example, of males (m) in patch i with, N male individuals is the result of N Bernoulli trials with probability $\mu_{m,i}$. The result has a binomial distribution with an expected value of

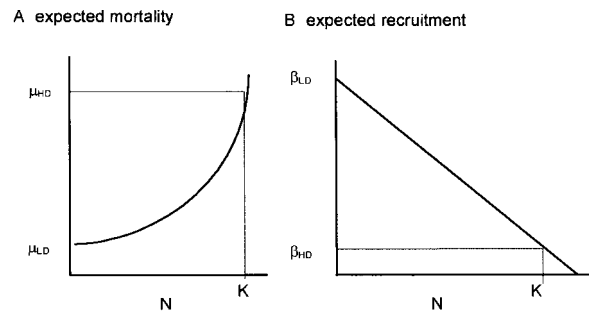


Figure A1: Expected mortality (A) and recruitment (B). K = carrying capacity; μ_{LD} , μ_{HD} = expected mortality at low and high density, respectively; β_{LD} , β_{HD} = expected recruitment at low and high density, respectively. High density refers to carrying capacity.

$$N_{m,i} \cdot \mu_{m,i}$$

The expected individual mortality μ_i in patch i consists of the following components:

$$\mu_i = \mu_{dd,i} + \mu_0,$$

where μ_0 refers to the annual background mortality in optimal habitat, in absence of density dependence, while $\mu_{dd,i}$ refers to the density-dependent component.

The normally distributed random variable μ_0 has a mean of μ_{LD} and a standard deviation of SD_μ . The standard deviation corresponds to the observed natural variation in mortality rate, excluding the impact of demographic stochasticity. It is obtained from a random variable ε , with a standard normal distribution, in the following way:

$$\mu_{0(t)} = \mu_{LD} + \varepsilon \cdot SD_\mu.$$

The density-dependent component of mortality is $\mu_{dd,i}$; the expected extra death rate in patch i with a density N_i (per sex), with optimal quality, and in absence of environmental variation. Density-dependent mortality increases exponentially (with coefficient z) with the ratio of density N_i to carrying capacity K_i :

$$\mu_{dd,i} = (\mu_{HD} - \mu_{LD}) \left(\frac{N_i}{K_i} \right)^z.$$

Reproduction parameters in METAPHOR refer to recruitment instead of birth. Birth is the number of offspring per female, measured (shortly) after the reproductive season. Recruitment indicates offspring that survive their first year of life, or reproduction on a yearly basis. Thus,

$$\text{recruitment} = \text{birth}(1 - \text{mortality}).$$

Recruitment (male offspring in this example) per reproductive female in patch i is calculated from the parameters β_{LD} (recruitment at low density) and β_{HD} (recruitment at high density) as follows:

$$\beta_{m,i} = \beta_{LD,m} - (\beta_{LD,m} - \beta_{HD,m}) \left(\frac{N_{rf,i}}{K_{f,i}} \right),$$

where $N_{rf,i}$ refers to the number of reproductive females in patch i and $K_{f,i}$ refers to the carrying capacity for females. In this application with territorial, monogamous animals, the expected number of nests (females reproducing) is the minimum of number of males, number of females, and carrying capacity (= number of territories).

Recruitment is subject to environmental variability and

$$A_{\text{mxd}} = 100$$

$$\delta_a = 0.15$$

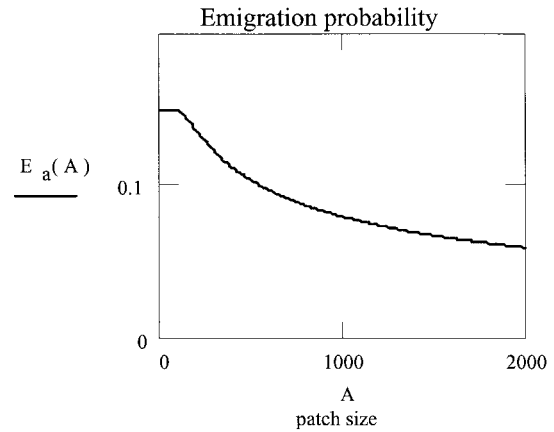


Figure A2: Emigration probability in relation to patch size

is influenced by both the annual fluctuation in mortality and the annual fluctuation in reproduction; a year can be a good reproduction year and a low mortality year, and so forth. To incorporate the impact of environmental stochasticity, the expected recruitment number is first transformed into birth number (using the equation above). A random variable (normally distributed with a mean of 0 and a standard deviation of SD_β) is added to the birth number; the result is transformed back to recruitment by multiplication with the survival of that year. Negative numbers are truncated to 0. The final value—recruitment adjusted for environmental noise in both recruitment and mortality—becomes the parameter of a Poisson distribution from which the number of recruits is obtained.

In METAPHOR, dispersal takes place once a year after mortality and reproduction. Dispersal in METAPHOR involves several steps to determine which (age, sex) individuals leave (emigration), in which direction they move (toward which patch), and what their chances are of arriving alive and settling in a target patch.

The number of emigrants, per age class and sex, leaving patch i is obtained from a binomial distribution with parameters $E_{i,a}$ and $N_{i,a}$ (ignoring the indices for male/female). The average (age-specific) individual emigration probability E_a is calculated for each patch as follows:

$$E_{a(A)} = \begin{cases} \delta_a \cdot \left[2 \cdot \sqrt{\frac{A_{\text{mxd}}}{A}} - \frac{A_{\text{mxd}}}{A} \right] & \text{for } A > A_{\text{mxd}} \\ \delta_a & \text{for } A \leq A_{\text{mxd}} \end{cases},$$

Table A1: Parameter values of the six model species (A–F)

Parameter	Symbol	A	B	C	D	E	F
Sex structure	...	Monogamous	Monogamous	Monogamous	Monogamous	Monogamous	Monogamous
Territoriality	...	Yes	Yes	Yes	Yes	Yes	Yes
Number of age classes	...	2	2	2	2	2	2
Area of maximum dispersal (ha)	A_{mxd}	1	1	1	1	1	1
Mortality at low density	μ_{LD}	.1	.1	.1	.4	.4	.4
Mortality at carrying capacity	μ_{HD}	.2	.2	.2	.5	.5	.5
Standard deviation of mortality	SD_{μ}	.0	.0	.0	.1	.1	.1
Exponent of density dependence	z	4	4	4	4	4	4
Maximum mortality allowed99	.99	.99	.99	.99	.99
Recruitment at low density	β_{LD}	.3	.3	.3	.8	.8	.8
Recruitment at carrying capacity	β_{HD}	.2	.2	.2	.6	.6	.6
Standard deviation of recruitment	SD_{β}	.0	.0	.0	.1	.1	.1
Dispersal probability (juveniles)	δ_j	.5	.5	.5	.7	.7	.7
Dispersal probability (adults)	δ_a	.1	.1	.1	.1	.1	.1
Number of territories per ha	...	1	1	1	50	50	50
Dispersal distance dependence	λ	.005	.00167	.0005	.005	.00167	.0005
Dispersal mortality (m^{-1})	μ_{δ}	.0025	.000835	.00025	.0025	.000835	.00025

Note: IAR = individual area requirements. Models are as follows: A = large IAR, short dispersal distance; B = large IAR, medium dispersal distance; C = large IAR, large dispersal distance; D = small IAR, short dispersal distance; E = small IAR, medium dispersal distance; and F = small IAR, large dispersal distance.

where A refers to the area of the source patch, A_{mxd} represents the area of maximum dispersal, and δ_a is the dispersal probability for age class a (fig. A2).

It is assumed that, moving from the border of a patch inward, individual dispersal probability will decrease. The A_{mxd} defines the maximum outer edge area of patches, where dispersal is unhampered. If the total area of a patch is smaller than A_{mxd} , the entire patch belongs to the outer edge area. When patch area is larger than A_{mxd} , average probability of emigration decreases with increasing patch area.

In this application of METAPHOR, a simple dispersal-direction algorithm is used in which only the distance to and the area of the target patch determine transition probability between patches. More sophisticated methods are available within METAPHOR. Let p_{ij} denote the transition probability between two patches, source patch i and target patch j . The algorithm is used to produce a matrix of transition probabilities from patch i to patch j :

$$P_{ij}.$$

Survival probability may be associated with the transition from source patch i to target patch j . This depends on the distance between the two patches D_{ij} (in meters):

$$e^{-\mu_{\delta} \cdot D_{ij}}.$$

Here, μ_{δ} denotes the mortality probability (m^{-1}) while dispersing.

The probability of selecting patch j as a target patch is proportional to the distance between source and target patch D_{ij} and the size of the target patch A_j :

$$p'_{ij} = A_j \cdot e^{-\lambda \cdot D_{ij}}.$$

The importance of distance is indicated by the value of λ . If $\lambda = 0$, then distance has no effect, and transition probabilities are directly proportional to target patch size. For large values of λ , all dispersers will move to the nearest patch. Patches are considered to be circles, and by calculating the distances, the center or border of patch i and j are used. Transition probabilities are normalized in order to sum to 1:

Table A2: Number of patches in relation to patch size (ha) and habitat percentage in the 14 simulation landscapes

Habitat percentage	Patch size (ha)				
	1	2	4	8	16
.5	50	25	13	7	...
1	...	50	25	13	7
2	50	25	13
4	50	25
8	50

$$p_{ij} = \frac{A_j \cdot e^{-\lambda \cdot D_{ij}}}{\sum_j A_j \cdot e^{-\lambda \cdot D_{ij}}}$$

Transitions from a patch to itself are not allowed ($j \neq i$). In this application, the disperser always settles in the arrival patch, independent of density or the presence of a partner.

In table A1, the parameter settings of the six model species are listed. The model species modules were derived from calibrated modules for two bird species: European bittern (*Botaurus stellaris*) and reed warbler (*Acrocephalus scirpaceus*). They represent the six ecological profiles (text; table 1) by incorporating the dispersal characteristics and area requirements.

The simulations were carried out in computer-generated landscapes of 100 km². Patch size was kept constant. The patches were distributed randomly by a landscape generator, keeping a minimal distance between patches of 1.5 times the home range size of the species with the largest area requirements. Fourteen different landscapes were used for each model species (table A2).

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